

HYDRATION IN THE SAND SHRIMP *CRANGON SEPTEMSPINOSA*: RELATION TO DIET

J. ROSS WILCOX¹ AND H. PERRY JEFFRIES

Graduate School of Oceanography, University of Rhode Island, Kingston, Rhode Island 02881

The sand shrimp *Crangon septemspinosa* Say 1818 is a common inhabitant of estuaries along the northwestern Atlantic from Newfoundland to eastern Florida (Squires, 1965; Williams, 1965; Price, 1962). The biology and ecology of the species is discussed by Embich (1973), Haefner (1969a, 1969b, 1970, 1971, 1972, 1973), Price (1962), Regnault (1970, 1971, 1972), Regnault and Costlow (1970), Sandifer (1975), Wilcox (1972), Wilcox and Jeffries (1973, 1974).

Hydration levels of crustaceans are affected by a variety of environmental and physiological parameters, and the literature detailing these factors is extensive (*e.g.*, Passano, 1960; Roberston, 1960). For example, molting of crustaceans has been scientifically documented for almost fifty years, and its endocrinology and ancillary process of growth is known in detail (Hoar, 1975).

The literature dealing with hydration in *Crangon* spp. is, however, quite limited. To document water content over a molt cycle, a generalized account suggested by Lockwood (1967) must be used. Thus, water content can vary from a high of 86% immediately after ecdysis (Drach Stage A₂) to a low of 59-61% during Drach Stage D. The time spent at high levels of hydration (greater than 80% water) is approximately 10% of a molt cycle. Weber and van Marrewijk (1972) negatively correlated percentage water content of muscle in *Crangon crangon* to increasing environmental salinity and determined that the shrimp possesses a relatively efficient water regulation system. Haefner (1969b) determined the osmoregulatory patterns of *C. septemspinosa* and found that all life stages were hyperosmotic in a dilute medium (15‰): adults were isosmotic and juveniles were hypoosmotic in 45‰; and all life stages were hypoosmotic in 30‰ sea water. Cuzon and Ceccaldi (1973) determined that starvation affects the hydration levels of *C. crangon* and that percentage water of muscle varied from $76.1 \pm 1.4\%$ to $77.7 \pm 0.5\%$ over the four-week study.

Adequacy of foods and their utilization are revealed by several indices in *C. septemspinosa*. Growth of the shrimp on a variety of diets over a period of weeks has been discussed by Wilcox and Jeffries (1974). Freshly prepared foods (*e.g.*, the clam *Merccenaria mercenaria*, the brine shrimp *Artemia salina*, hard-boiled egg) promoted better growth than dried foods (*e.g.*, *Merccenaria*, *Artemia*, *Crangon*, fish meal, copepods). This difference in growth was attributed to loss of olfactory attractants upon drying. In this study, the effects of nutrition on hydration in *C. septemspinosa* were determined.

¹ Present address: Florida Power and Light Company, Environmental Department, P.O. Box 013100, Miami, Florida 33101.

MATERIALS AND METHODS

In all experiments to relate hydration to nutritional status, shrimp of both sexes and greater than 25 mm in length were seined from Pettaquamscutt River, Narragansett, Rhode Island (41° 26' 55" N and 71° 27' 05" W; water temperature 20° C; salinity 27–29‰) during the summer and fall of 1970 and 1971. Two laboratory groups were placed in 300-liter tanks with a sand substratum. Sea water (20° C, 30–32‰) from Narragansett Bay was filtered through glass wool to remove particulate material and was circulated through the tank at 1 liter/min. All other experiments had the same water source and flow rate. In one laboratory group of 29 shrimp, fresh tissues of *Mercenaria* were given *ad libitum* for a total of seven days (fresh tissue: *Mercenaria* opened 15 min before feeding and all soft tissue diced). Uneaten portions were removed prior to the daily feeding period. No food was given to the second laboratory group of 50 shrimp. A third group of 80 shrimp collected in the field and analyzed for hydration served as control.

Shrimp were blotted to dryness on paper towels, individually weighed to the nearest 0.1 mg (wet weight), freeze dried, and then reweighed. Hydration was expressed as a percentage of the dry weight to wet weight.

Fisher's Least Significant Difference (LSD) was used for pair-wise comparison of groups with multiple means (Fryer, 1966). If two means differed by the LSD, they were statistically different at $P = 0.05$. Student's *t*-statistic for unequal variances was used for pair-wise comparison of two means (Fryer, 1966).

Further hydration-feeding experiments were made with 225 shrimp held in a tank (2 × 0.25 × 0.25 m) divided into 12 compartments, each with a sand substratum. This experimental design allowed four replicates of the three feeding regimes. Filtered sea water entered one end and drained at the opposite end. Diets were as follows: 2.2% agar in sea water (Bactoagar, Difco Laboratories, Detroit, Michigan); homogenized freeze-dried tissues of *Mercenaria* in agar (6 g tissue in 30 ml of 2.2% agar); and no food. Each diet was prepared as a batch and smaller portions were given *ad libitum* on a daily basis for seven days.

In a final set of hydration-feeding experiments, 14–24 shrimp were held in 300-liter tanks with a sand substratum, a screen partition dividing the tanks in half (control group on one side and experiment group on the other), filtered sea water, and daily *ad libitum* feeding. Control diet for each trial was fresh tissues of *Mercenaria*. Each experimental diet was prepared as a batch by mixing 6 g of dried tissue in 30 ml of 2.2% agar; smaller portions of the diet were then fed to the shrimp for fourteen days. The amount of food ingested in each trial was estimated by the amount removed prior to the next feeding period. Foods in the experimental diets were as follows: 1) soft tissues of *Mercenaria* homogenized and freeze-dried; 2) fish meal of hake (*Urophycis* spp.) obtained from Point Judith, Rhode Island; 3) *C. septemspinosa* taken from Pettaquamscutt River, freeze-dried, and ground with a mortar and pestle; 4) blocks of frozen adult *Artemia* obtained from Metaframe Co., San Francisco, California and freeze-dried; 5) calanoid copepods collected over a period of a year in Narragansett Bay and freeze-dried; 6) beef liver purchased at a supermarket, homogenized, and freeze-dried; 7) 2.2% agar made in sea water; 8) marine yeast (*Candida sake*) isolated from macro-vegetation in tide pools at Narragansett, Rhode Island and grown in a malt extract broth (25 g/liter sea water), and freeze-dried; 9) Baker's yeast obtained from

TABLE I

Hydration levels of *C. septemspinosa* were determined after seven days of feeding. The LSD for each combination of pairs was: $LSD_{12} = 1.03$; $LSD_{13} = 0.86$; $LSD_{23} = 1.11$; $P = 0.05$. The environmental parameters were: water temperature 20°C ; laboratory salinity 30–32 ‰; field salinity 27–29 ‰.

Group	Food	$\bar{x} \pm \text{s.d.}$ Per cent water	N
1 Field	Natural diet	70.74 ± 2.66	80
2 Laboratory	Fresh tissues of <i>Mercenaria</i>	72.74 ± 2.36	29
3 Laboratory	Starved	74.84 ± 1.91	50

Fleishmann's Yeast, Standard Brands, Inc., New York; 10) bacteria, probably of a *Pseudomonas* group, isolated from Narragansett Bay sea water and grown in 1.0 g yeast extract and 1.0 g trypticase/liter sea water; 11) TetraMin (dried tropical fish food) obtained from TetraKrafteWerke, West Germany; 12) *Spartina alterniflora* detritus and attached microflora, 0.500–0.017 mm particle size, collected at Bissels Cove marsh in North Kingston, Rhode Island.

In an ancillary experiment to determine hydration levels of recently molted shrimp, males and nonovigerous females of greater than 25 mm in length were collected during July 1970 from Pettaquamscutt River. Each shrimp was placed in an individual 10-liter container provided with sand substratum, unfiltered sea water, and fresh food (tissues of *Mercenaria*) given *ad libitum*. Nine shrimp were analyzed for water content within 24 or 48 hrs of molting; 23 individuals that had not molted in the last 96 hrs served as control.

RESULTS

Significant differences in hydration were found among a field group, a laboratory group that was fed, and a laboratory group that was starved (Table I: LSD, $P = 0.05$). The difference between the field group and the laboratory-fed group could be attributed either to environmental differences or to capturing, handling, and keeping. Because both laboratory groups were maintained under identical conditions, the difference in hydration levels between Group 2 and 3 was presumably due to lack of food.

Groups fed fresh tissues of *Mercenaria* as opposed to freeze-dried tissues of *Mercenaria* in agar had no significant differences (Table II: Trials 1–3, LSD, $P = 0.05$). Due to varying natural salinity during these trials, results should not be compared between one trial and another. In Trial 4 (Table II), there was a significant difference between the fed groups (freeze-dried *Mercenaria* in agar as opposed to agar; LSD, $P = 0.05$), and a difference (LSD, $P = 0.10$) between the group fed tissues of freeze-dried *Mercenaria* in agar and the starved group. However, there was no significant difference in hydration (LSD, $P = 0.05$) between the group fed agar and the starved group. Approximately 75% of the agar fed to the shrimp in Trial 4 was recovered prior to the next feeding period. Thus, the shrimp ingested only small amounts of this food on a daily basis, and this group, for all practical purposes, was subjected to nearly identical conditions as the starved

group. Therefore, elevated levels of hydration appear to be related to low levels of ingestion or complete lack of food (Table II: agar, Trial 4; starved group, Trials 1-4).

In another experiment (Table III), foods for Trials 1-12 were selected which would be similar to those available in nature. Sand shrimp which were fed tissues of marine organisms (*i.e.*, *Mercenaria*, fish meal, *Crangon*, *Artemia*, copepods) did not hydrate, while shrimp fed foods from terrestrial, plant, or microbial sources (*i.e.*, beef liver, agar, marine yeast, Baker's yeast, bacteria, fish food, and *Spartina* detritus) did hydrate. On a short-term basis, marine foods (*i.e.*, foods of Trials 1-5) were ingested to a greater extent than the foods of Trials 6-12. Again, elevated levels of hydration appear to be related to low levels of ingestion.

Hydration ($\bar{x} \pm \text{s.d.}$) in shrimp that had molted in the last 24 and 48 hrs was $77.71 \pm 1.24\%$ (Group 1, $n = 6$) and $76.85 \pm 0.41\%$ (Group 2, $n = 3$). Shrimp that had not molted in the last 96 hrs had hydration levels of $71.70 \pm 2.42\%$ (control; Group 3, $n = 23$). The LSD for each combination of pairs was $\text{LSD}_{12} = 3.30$, $\text{LSD}_{13} = 2.14$, $\text{LSD}_{23} = 2.86$ ($P = 0.05$). Hydration, therefore, in recently molted shrimp was significantly greater than the control. Even after 48 hrs hydration was elevated but declining from a post-molt high of 77.71%.

DISCUSSION

Hydration of *C. septemspinosa*, as well as any other crustacean, is affected by many physiological processes. High levels of hydration occur after ecdysis and

TABLE II

Hydration levels of C. septemspinosa were determined after seven days of feeding. The clam and agar diet was freeze-dried tissues of Mercenaria in agar and the clam diet was fresh tissues of Mercenaria. The LSD was calculated at P = 0.05. The environmental parameters were: water temperature 20° C; salinity 30-32 ‰.

Food	N	$\bar{x} \pm \text{s.d.}$ Per cent water	LSD
Trial 1			
Clam (control)	24	72.47 ± 1.85	1.01
Clam + agar	24	72.65 ± 1.59	
Starve	24	74.30 ± 1.78	
Trial 2			
Clam (control)	22	70.44 ± 2.07	1.16
Clam + agar	22	70.75 ± 1.93	
Starve	22	73.32 ± 1.72	
Trial 3			
Clam (control)	20	74.58 ± 2.42	1.25
Clam + agar	20	74.85 ± 1.28	
Starve	20	76.33 ± 2.03	
Trial 4			
Clam + agar (control)	19	74.66 ± 2.41	1.82
Agar	19	76.88 ± 2.63	
Starve	19	76.33 ± 3.20	

TABLE III

Hydration levels of *C. septemspinosa* were determined after fourteen days of feeding. The control food was fresh tissues of *Mercenaria*. See the text for the source and the preparation of the foods. The level of significance was: $P < 0.05$, $P < 0.01$, and *ns* (not significant). The environmental conditions were: water temperature 20°C ; salinity 30–32 ‰.

Trial	Food	$\bar{x} \pm \text{s.d.}$ Per cent water	DF	<i>t</i> -statistic	Level of significance
1	Control Freeze-dried <i>Mercenaria</i>	74.35 ± 2.17 73.39 ± 1.66	16	1.06	<i>ns</i>
2	Control Fish meal (dried)	71.72 ± 2.25 72.29 ± 1.58	18	0.66	<i>ns</i>
3	Control Freeze-dried <i>Crangon</i>	71.10 ± 2.64 71.05 ± 2.61	20	0.04	<i>ns</i>
4	Control Freeze-dried <i>Artemia</i>	72.25 ± 3.10 73.83 ± 2.51	24	1.42	<i>ns</i>
5	Control Freeze-dried copepods	74.61 ± 2.79 76.08 ± 0.87	14	1.43	<i>ns</i>
6	Control Freeze-dried beef liver	70.87 ± 3.05 73.30 ± 2.36	20	2.09	≤ 0.05
7	Control Agar	70.44 ± 2.54 76.26 ± 1.30	22	7.08	≤ 0.01
8	Control Freeze-dried marine yeast	70.83 ± 2.54 76.14 ± 2.21	22	5.46	≤ 0.01
9	Control Baker's yeast (dried)	72.59 ± 3.26 76.35 ± 1.94	16	2.97	≤ 0.01
10	Control Freeze-dried marine bacteria	70.62 ± 2.56 77.82 ± 1.91	16	6.76	≤ 0.01
11	Control TetraMin (dried fish food)	70.72 ± 1.56 75.82 ± 2.32	16	5.47	≤ 0.01
12	Control Freeze-dried <i>Spartina</i> detritus	74.11 ± 2.92 79.81 ± 1.20	18	5.74	≤ 0.01

decrease 48 hrs following a molt. Lockwood (1967) and Passano (1960) also determined that maximum levels of hydration occurred immediately after ecdysis and were of short duration, whereas low levels of hydration occurred during the remainder of the molt cycle.

Ecdysis and its attendant cycle of hydration is a variable that can never be satisfactorily factored out of an experiment. The problem, however, can be minimized by using a sufficient sample size. Since a crustacean spends approximately 10% of its molt cycle at elevated water levels (Drach Stage A_2 ; Lockwood,

1967), the chances of a control or experimental shrimp being harvested in Drach Stage A₂ are approximately 1 in 10. The number of shrimp used in each experiment was 14–80. Statistical presentation of hydration-feeding results would, therefore, minimize the confounding effects of ecdysis.

Meixner (1969) observed that a rise in water temperature accelerated growth, as well as the molting rhythm of *C. crangon*. Wilcox and Jeffries (1973) concluded that growth rate is a positive function of water temperature and a negative function of size (i.e., larger shrimp grow slower than smaller shrimp). For instance, Wilcox (1972) reported that at an average water temperature of 13° C the intermolt period of *C. septemspinosa* was as follows: 2 weeks for 15–29 mm length shrimp; 3 weeks for 30–39 mm shrimp; and 4 weeks for 40–49 mm shrimp. The size of shrimp used in the present experiments was greater than 25 mm and the water temperature was 20° C. The test period was short (1 or 2 weeks) compared to an extrapolated 2–3 week intermolt period for 25 mm or larger shrimp at 20° C. Therefore, although size and water temperature affect the molting cycle in *Crangon*, by selecting a short experimental period, the confounding effects of the molt cycle may also be minimized.

Hydration of *C. septemspinosa*, upon transfer from field to laboratory (i.e., a salinity increase; Table I), is not simple osmosis, because internal water content would be expected to decrease on transfer to higher salinity (Hoar, 1975). Moreover, since Weber and van Marrewijk (1972) have determined that *C. crangon* is an efficient regulator in the range of salinity encountered, minor salinity changes (ca., 3‰) would probably not tax water regulation of *Crangon* spp. In this case, perhaps hydration is a response to capturing, handling, and laboratory maintenance.

Hydration could result either from lack of nutrient input, or the inability of the shrimp to digest and metabolize the ingested food. Wilcox and Jeffries (1974) have suggested that the limitation of feeding for *C. septemspinosa* lies not with its ability to digest the food, but with the stimulated response of food location and ingestion. Based on our present results, starvation or low food input is a probable explanation for hydration. Examples of "poorly ingested" foods would be agar (Table II: Trial 4) and foods from terrestrial, plant, or microbial sources (Table III: Trials 6–12). Shrimp presented these foods, on a short-term basis, are presumably on a marginal existence and catabolizing metabolic reserves. Thus these shrimp, for all practical purposes, respond the same as starved shrimp.

Foods from terrestrial, plant, or microbial origins, perhaps, lacked water-soluble components that attract shrimp and stimulate ingestion. Observations by Wilcox (1972) on the feeding behavior of *C. septemspinosa* showed that they located food in a homing zig-zag path (klinotaxis; see Hoar, 1975, p. 500). Similar types of homing behavior are also common for other crustaceans (Pardi and Papi, 1961). Other investigators feel that initiation of feeding chiefly depends on chemical stimuli (Barber, 1961; Nicol, 1967). Lindstedt (1971), for example, found that two chemical activators were necessary for a complete feeding response in the sea anemone. One activator initiated contraction and bending of tentacles, the other controlled ingestion. Gurin and Carr (1971) concluded that specific proteins were necessary to induce feeding in the marine snail *Nassarius obsoletus*. Drying, either by heat or freeze-drying, apparently modifies the food, as suggested by Wilcox and Jeffries (1974). Sublimation or heat, besides removing water, may have removed or altered sensory attractants, which stimulate feeding. Foods

of a terrestrial, plant, or microbial origin may have been more effectively stripped of attractants by freeze-drying, if the attractants were present at all.

Regnault, Campillo, and Luquet (1975) reported better survival and weight increases of the shrimp *C. crangon* and *Palaeomon serratus* when fed a hydrated artificial diet (pastes) contrasted to pelleted artificial foods. They also felt that the hydration level of the diet may have an influence on the ingestion rates for these shrimp.

Based on the results of the hydration experiments (Tables I-III), tissues of *Mercenaria*, either fresh or freeze-dried, provided nutrients to *C. septemspinosa*. Similarly, Wilcox and Jeffries (1974) concluded that these two foods provided nutrients to the shrimp on a long-term basis. There was a difference, however, in growth performance between the fresh and dried diets, which was attributed to olfactory quality.

If starved or given agar (Tables I-III), the shrimp hydrate in a short period of time. Wilcox and Jeffries (1974) demonstrated that agar provided nutrients to *C. septemspinosa* but at a lower rate when contrasted with foods derived from marine sources. Wilcox (1972) also noted hepatopancreal shrinkage in *C. septemspinosa* during starvation. Cuzon and Ceccaldi (1973) observed that starved *C. crangon* metabolized glucides first, lipid reserves next, and proteins last. Hydration of muscle tissue increased over the experiment. Presumably as food reserves are metabolized and tissues shrink, water replaces tissues to maintain internal turgidity.

Although terrestrial, microbial, and plant foods of Trials 6-12 (Table III) caused hydration of *C. septemspinosa* on a short-term basis (two weeks), Wilcox and Jeffries (1974) showed that these same foods provided nutrients sufficient for growth and survival over eight weeks, but at reduced rates when contrasted to foods derived from marine sources. Also, the maintenance of *C. septemspinosa* feeding on some of these same foods may have been marginal since Wilcox (1972) reported hepatopancreal atrophy. Additionally, starvation of *Crangon* spp. can still result in molting and growth (Lockwood, 1967; Wilcox and Jeffries, 1974). Thus, the difference in response on identical foods may reflect the sensitivity of the hydration/growth indices.

Nutritional experiments using growth and survival data as criteria of performance require long-term studies. Even lengthy studies may be misleading, because some crustaceans can continue to grow under nutritional stress. Perhaps egg-laying capacity would be an equivalent or more sensitive long-term index (Lockwood, 1967). Hydration, however, may be a short-term, sensitive, and expedient indicator of nutritional status in *C. septemspinosa* and other crustaceans.

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SUMMARY

Tissue hydration in the estuarine sand shrimp *Crangon septemspinosa* is correlated with nutritional conditions. Hydration levels of shrimp who are ingesting

food remain normal. In starved shrimp or in individuals who are not ingesting adequate amounts of food, hydration levels are high. Presumably, water replaces metabolized tissues.

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